Some Aspects of the Ecology
and Nest Microclimatology of the Meat Ant,
Iridomyrmex purpureus (sm.)

By G. Ettershank*

ABSTRACT: The nest of the meat-ant (*Iridomyrmex purpureus*) was studied in an arid region of Australia. Temperature (above and below soil level), heat flux, moisture and respiratory gases were measured, and soil characteristics determined. These enabled the conditions in which ants live in the nest to be described. The possibility of treating the nest as a natural calorimeter was examined and rejected, but a method of determining nest metabolism by collection of gas samples under a hood on the nest was utilized; this method also led to a back-calculated estimate of population. The varying nature of the nest 'decoration' was considered and some conclusions drawn on its functions.

INTRODUCTION

The meat ant, *Iridomyrmex purpureus* (Sm.) lives in nests in the ground. Details of the biology and nest structure are given elsewhere (Ettershank, 1968; Greaves, 1939; Duncan-Weatherley, 1953; Anon., 1956). The nests vary from small, rather inconspicuous mounds with a single opening to extensive nests up to 10·7 m across, and 0·6 m high with 1061 entrance holes (Anon., 1956). In many areas these nests are covered with small pebbles or ironstone nodules about 2-4 mm diameter, or twig fragments, gumnuts or grass stem fragments. Most of the galleries are concentrated in the upper 15 to 25 cm of the mound, but some of the galleries and shafts may extend two to three m into the ground. The nests are situated on well drained sites, usually associated with trees, but never in situations where the tree canopy is closed. The workers forage on trees, collecting honey-dew from homopterous insects and nectar from floral and extrafloral nectaries; they also scavenge dead and dying insects. The species occurs over much of Australia, from heavy rainfall areas through to semi-desert with an average annual rainfall of 20 cm.

The present paper describes an investigation into conditions within the nest of the meat ant—involving measurement of temperature, radiation, heat and water movement, humidity and respiratory gases—in an arid mallee-scrub area 112 km south of Broken Hill, N.S.W. The aim of the project was to obtain information on the nest microclimate, and to ascertain whether temperature measurements could be used to estimate the overall metabolism of the nest (that is whether the nest could be treated as a natural calorimeter, Engelmann, 1966), and whether metabolism could be estimated by a gas analysis method.

Previous studies of temperature in ant nests have been conducted purely for their own sake, and all relate to species in Europe and North America. No previous study in Australia has been concerned with nest microclimate, water status or energetics. Duncan-Weatherley (1953) made surface observations on nest form, but was more concerned with behavioural aspects, particularly those relating to foraging. Greaves (1939) and Anon. (1956) were primarily concerned with the control of the meat ant as a pest species, a status it acquires in only relatively few places. Ettershank (1968) examined the three dimensional relations of the gallery system, and found that each entrance on the nest opened into a separate set of galleries; nest entrances were found to occur in a somwhat regular pattern. The only other extensive study of an Australian ant species is that of Saunders (1967, 1969) on the effects of *Aphaenogaster* spp. on pasture grasses in North Queensland. There is also a somewhat inconclusive study by Nel (1965) on the effects of temperature

* Department of Zoology, Monash University, Clayton, Victoria 3168, Australia.

and humidity on water loss in workers of the meat ant.

Ecologically equivalent types of nests to that of the meat ant are those of the American harvester ants of genera *Messor, Veromessor* and *Pogonomyrmex*. Golley and Gentry (1964) attempted to estimate energy flow in *Pogonomyrmex badius* nests in South Carolina; in the course of this study soil temperatures at various depths from 150 cm to the surface were taken for three days in January and July, but these are not reported in their paper in detail, nor is their technique given. They considered the summer and winter soil temperatures at 90-100 cm depth to be a 'rough estimate' of the temperature at which the ants were living underground. A graph showing daytime surface temperatures in July, May, October and February, and activity on the mound indicates that the ants became active in the morning when the surface temperature reached about 32°C, but later in the day the ants were active between 15 and 50°C. Data for temperatures at surface, 30, 60 and 90 cm were taken only at four-hourly intervals for a 'typical' summer and winter day; there is, moreover, a disparity between their 'typical' surface temperatures and those shown in their graph. They also undertook an analysis of productivity of this ant. A mark/recapture technique was attempted to estimate populations, but total excavation of colonies showed that only a portion (about 10%) of the population foraged and was thus available for marking. Nest populations were estimated at between 4,000 and 6,000, and there were 0·0027 nests per sq m. They calculated that 14·2 Kcal to 47·7 Kcal m^{-2} yr^{-1} was used in respiration, and 0·09 Kcal m^{-2} yr^{-1} of new biomass was produced each year. This ant is considered to be graminivorous; the field produced 22 Kcal m^{-2} yr^{-1} of seeds, so their estimates of gross productivity broadly spanned the primary productivity: they thought the difference could be made up in insectivory. Other consumers were the sparrow (4 Kcal m^{-2} for a 150 day season) and the mouse (7-17 Kcal m^{-2} yr^{-1}). Golley and Gentry point out that the primary sources on which these estimates are made are not equally reliable. Density per nest and soil temperatures were based on only a few observations, and the 'estimates of production are least reliable'. To this list should be added oxygen consumption, as this was based on the uptake of a relatively few workers in a simple, non-replacement respirometer. A graph of their data for oxygen consumption versus temperature shows the usual exponential rise, but the data were not transformed to logarithms and a regression line fitted, which is the usual procedure in such cases. This study should be regarded as no more than a first approximation—and yet it is the only one of its kind for ants to date, and indeed such analyses are relatively uncommon for any communities or smaller groups of taxa (Engelmann, 1966).

The behaviour of soil, and particularly of the moisture it contains, when exposed to solar radiation has been intensively studied by the methods of agricultural physics. Geiger (1965) discusses in detail the present state of knowledge of heat flow in soils, temperature stratification in the ground, and temperature fluctuation on a diurnal and annual scale. Geiger (1965) and Rose (1966) discuss a mathematical model for heat flow in an idealized soil, based on the assumption that temperature change at the soil surface is a sinusoidal function. Under these conditions, the temperature at any depth may be readily predicted. While this condition is met fairly well on an annual basis, it is not met in diurnal temperature change; not only is the assumption of a sinusoidal cycle violated, but changes in thermal conductivity with depth are not allowed for in the model. For an ideal soil, the daily temperature fluctuation at 35 cm falls to 5% of its surface value, taking a typical value of the thermal conductivity. For the annual wave, the corresponding depth for 5% for the surface fluctuation is 6·7 m. Geiger (1965) gives several examples of soil temperature profiles for annual and diurnal cycles, and discusses the modifying effects of vegetation.

Slatyer and McIlroy (1961) consider energy flow in soils further; it can be shown that the total solar energy arriving at the ground surface, R_s, may be partitioned as follows:

$$R_s(1-a) = R_L + G + H + LE \text{ where}$$

R_s = flux density of total short-wave radiation
a = albedo
R_L = net flux density of long-wave radiation emitted from the surface
G = heat flux density into the ground
H = actual heat flux density into the atmosphere
L = latent heat of vaporization of water
E = evaporation rate, including transpiration.

Some of these may be measured fairly easily. A net radiometer records incident radiation on its upper surface (R_s), and on its lower surface it subtracts reflected shortwave radiation ($R_s \times a$) and emitted longwave radiation R_L; the radiometer output is thus an electrical analogue of net radiative input. The heat-flux density moving down into the ground (conventionally considered positive), or back towards the surface (negative) may be measured by heat flux plates. The latent heat of vaporization of water being known, this leaves

two unknowns (H and E), the sum of which may be readily obtained from the other components. The component of major interest here is E, the evaporation rate, so the problem comes down to partitioning the remaining energy into the amount used in warming the air above the soil (H) and that used to supply the latent heat, usually called respectively the sensible and latent fluxes. This problem was considered by Bowen in 1926, and the so-called Bowen ratio provides a method of partitioning by the Energy Balance Method; Slatyer and McIlroy (loc. cit.) describe the necessary instrumentation and working methods, and provide the necessary tables and a sample work sheet for computation. The data required are wet and dry bulb temperatures at two levels above the surface being studied, as well as the radiation flux described above.

MATERIALS AND METHODS

Suppliers of equipment referred to by superscript numbers in this section are: 1. Yellow Springs Instrument Co., Yellow Springs, Ohio, U.S.A. 2. Swissteco Pty. Ltd., Hawthorn, Vic., Australia. 3. Middleton and Co. Pty. Ltd., South Melbourne, Vic., Australia. 4. Curtis Instrument Co. (Model 150-SP), Mount Cisco, N.Y., U.S.A. 5. The Tintometer Ltd., Salisbury, England, U.K.

1. LOCALITY

Nests of the meat ant are found in open spaces in the sparse mallee scrub which covers a series of old, low sandhills running generally E.-W.; the area is known locally as the South Ita Sandhills, and is in the northern part of Coombah Station, 112 km due south of Broken Hill. Brough & Ettershank (unpublished data) found by line transect analysis that the mallee (*Eucalyptus dumosa*) canopy overlaid 15% of the ground, and other tree species less than 1%; porcupine grass (*Triodia* sp.) covered 23% of the ground, and all other grasses and herbs less than 1%. Nests are, consequently, situated adjacent to the trees on which the workers forage, but they are shaded, at most, only in the early morning and late evening. The ants clear all seedlings and wind-carried plant parts from on and around the nest—the ground around well established nests may be clear for a distance of one to three metres from the nest margin. In addition, due to the clumped life-form of *Triodia*, there are often large, naturally bare areas around nests.

2. TEMPERATURE MEASUREMENT

Temperatures were measured with a six-channel, multirange YSI Telethermometer[1] fitted with an additional switching box to accommodate ten further probes. The instrument can be read reliably to 0·05°C from 0°C to 50°C. The thermistor probes used were YSI type 401, which have

a heavily insulated lead, and the thermistor bead enclosed in a radiation-reflecting cap.

The probes for soil measurements were carried across to the required position by taping them to a steel wire stretched across the nest, at least 10 cm above the surface. They were always inserted on the northern (equatorial) side of the wire, using an instrument consisting of a grooved steel rod, 90 cm long, fitting snugly inside a slotted aluminium tube.

A small detachable collar caused the tube to protrude 20 mm past the end of the steel rod, and this retained a small, pointed, disposable plastic cap which protected the thermistor probe during insertion. In use, the lead was first lubricated with talcum powder, laid in the groove and the tube rotated to cover it. The entire assembly was inserted into the nest or soil to the required depth; the small collar at the base of the steel rod was removed and the aluminium tube retracted from the plastic tip. The inner rod was then rotated 180° so that the lead could be peeled from the groove and held firmly to the ground while the inserter was removed. The small hole remaining was filled with soil tamped in with a thin dowel.

To ascertain if there was appreciable heat pick-up in the exposed part of the lead, two probes were placed side by side in the soil. The lead of one was brought vertically to the soil surface and back to the measuring instrument taped to a wire as described above; the second was brought horizontally back to the measuring instrument in a trench 5 cm deep, and then soil was packed firmly around both leads. Readings taken every fifteen minutes from 10 a.m. until 2 p.m. on a clear summer day gave the same temperature for each probe throughout.

Air temperature leads were fitted with tubular, chromed-brass radiation shields. Wet bulb temperatures were obtained with a fast response 'banjo' thermistor probe covered with lens tissue and wetted at the start of each reading series with distilled water applied with a dropper. It was contained in a radiation shield and aspirated with a fan driven by a battery-powered motor. Its performance was compared with that of a standard Assman ventilated psychrometer, and it gave results accurate to within the accuracy of the instrument.

3. RADIATION AND HEAT FLOW

Net radiation at one metre above the nest was recorded with a Funk Net Radiometer[2] (Platt and Griffiths, 1964), fitted with polythene shields and ventilated with dry air. Heat flux in the soil was measured with flux plates[3] (Philip, 1961), connected in parallel to obtain average values for the nest. The plates were buried to a depth of 5 cm in the

K

nest surface between entrances, and the soil re-packed tightly on top of them. The leads were run underground to the nest margin by the shortest route. The ants repaired the damage to the nest surface, and the position of the soil plates was not easily determined by inspection.

As both the radiometer and the flux plates are thermopile devices, with low internal resistance, they should not be connected to low impedance measuring devices because of the Peltier cooling and other errors generated in such a circut. Each was connected to a separate, integrated-circuit amplifier, with an input impedance of 10K ohms and an amplification of $\times 100$ for the radiometer and $\times 1000$ for the flux plates. The electronic components were housed in a sealed box and buried $0 \cdot 6$ m in the ground to obtain reasonable temperature stability (daily variation $1 \cdot 0°C$). Read-out was by a taut-band, multi-ranged meter (1, $2 \cdot 5$ and 10 volt ranges), with provision for connecting a chart recorder, and for integrating over time using mercury coulometers.[4]

4. RELATIVE HUMIDITY.

Two long (25 cm) hollow needles were inserted into galleries in the nest, and air samples were aspirated from these using a 100 cm^3 syringe, containing a piece of BDH cobalt thiocyanate paper (Solomon, 1957). The air sample was allowed to equilibrate for 30 minutes, and the relative humidity determined by comparison between the paraffin-mounted test paper and standards on a colour wheel in a Lovibond Opaque Comparator[5]. Samples for comparison were also drawn from a needle in a 'synthetic gallery', constructed at a depth of 20 cm by drilling a $2 \cdot 5$ cm hole, inserting a needle carrying a $2 \cdot 5$ cm plastic disc so as to leave a cavity about 4 cm deep, and packing soil on top. Finally, six perforated plastic vials containing cobalt thiocyanate papers were buried at a depth of 20 cm for several days before they were retrieved. All humidity determinations were corrected for temperature using tables (attributed to M. E. Solomon) supplied by the manufacturer.

5 RESPIRATORY GASES

Air samples were aspirated from the nest and soil through the needles described above. Samples were also taken from a hood with metal sides and clear plastic top, measuring $25 \cdot 6$ cm on each side and $5 \cdot 1$ cm high, fitted with a fan on a shaft protruding through the top (with which the air in the hood could be stirred) and a rubber port to withdraw air samples with a 10 cm^3 syringe. The volume of the hood, determined by filling it with water, was 3,350 cm^3. The hood was pressed down firmly onto the surface of the soil or the nest, and moved about slightly to obtain a close fit. Samples were drawn after 25 minutes; gas in the hood come into equilibrium after 30 minutes, as the rate of uptake dropped off after this time. Analyses were carried out in the field with a Scholander Gas Analyzer (Scholander, 1947), fitted in an insulated jacket and with the water bath controlled by a thermostatically-controlled 12-volt heater and stirrer. Sodium sulphate crystallized out of the acid rinsing solution at low temperatures, and it was necessary to keep the bulk supply in a warmed, insulated box.

Collection of gas samples under a hood is a practice established in agriculture, where it is used to obtain estimates of carbon dioxide production on plots (Koept, 1952; Ellis, 1966). In this technique, the hood sits on a collar which is permanently positioned at the collection site; carbon dioxide is drawn into an analysis vessel, dissolved in alkali and electrolytically titrated. The use of a permanent collar was tried in nests at Bacchus Marsh, but caused such perturbation that it was abandoned: even after several days, the ants were still trying to excavate the collar if it was not buried deeply, or bury it if it was. The consolidated surface of the nest provides a good contact for the hood provided some care is taken to scrape off any high spots by moving the hood back and forth.

Oxygen consumption rates for single ants were obtained using an electrolytic replacement respirometer (Ettershank, unpublished).

6. SOIL CHARACTERISTICS

Soil moisture was determined gravimetrically (Slatyer & McIlroy, 1961); samples were collected into aluminium containers, care being taken to exclude ants from the samples. Three nests were sampled on an 8×8 grid, $30 \cdot 5$ cm between sample points. Additional samples were collected during other phases of the study as required.

The specific gravity of the soil was obtained by a method based on that of the Standards Association of Australia (1966). A known weight (W1) between 80 and 100 grams of oven dried soil was placed in a 500 ml volumetric flask and the flask nearly filled with de-ionised water. Air was removed under vacuum and the flask filled to the calibration mark with de-aired water. The flask plus soil and water was weighed (W2), emptied, cleaned, filled to the calibration mark with de-aired, de-ionised water and reweighed (W3). The specific gravity is given by the expression W1/(W1 — W2 + W3).

A more realistic measure for soils is the bulk density, i.e. weight per unit volume of soil, including natural voids. As the nest soil contains

tunnels made by the ants, the usual sand replacement method could not be used, and a volumetric method (Slatyer & McIlroy, 1961) was applied. Blocks of soil were excavated and brought to the laboratory. Loose soil was removed from the ant galleries (when applicable), and the sample was dried and weighed. It was then sprayed with lacquer to retain its shape, redried and dipped in molten paraffin wax at 105°C, then allowed to drain in the same oven for ten minutes, during which time the wax was drawn into the surface of the soil block. On cooling, a consolidated, waterproofed block resulted. The volume of each block was determined by immersion in a beaker of water containing a little 'Tween 80' detergent. Adhering bubbles were removed by a jet of water from a pipette, and a hook gauge arranged so that its tip just dimpled the surface. The block was removed and drained carefully back into the beaker. Water was added from a burette to restore the level, giving the volume of the block.

The specific heat of the soil was obtained by simple calorimetry. The calorimeter consisted of a light aluminium can of 220 ml capacity, fitted with a polyurethane foam jacket and a clear plastic lid through which a precision mercury-in-glass thermometer was inserted. About 50-70 grams of oven-dried soil was accurately weighed and placed in an oven at 105°C. The calorimeter was cleaned, dried and weighed, placed in its jacket and 100 ml of distilled water added. The calorimeter and water were allowed to equilibrate, and the temperature taken. As quickly as possible, the soil was removed from the oven and tipped into the calorimeter, the lid placed on and the mixture stirred with the thermometer. The temperature rose until soil, water and can were in equilibrium, when the temperature was read. Then

$$C_s = \frac{(W_{al} C_{al} + W_w) (T_{eq} - T_w)}{W_s (T_s - T_{eq})} \text{ cal gm}^{-1} \text{ deg C}^{-1}$$

where

W_{al} = weight of calorimeter can
C_{al} = specific heat of aluminium
W_w = weight of water (specific heat = 1)
W_s = weight of soil
C_s = specific heat of soil
T_w = initial temperature of the water
T_s = initial temperature of the soil
T_{eq} = equilibrium temperature of the mixture.

The thermal capacity, defined as the heat required to raise the temperature of 1 cubic centimetre of soil one degree Celsius (Geiger, 1965) is the product of the specific heat and bulk density, and has units cal cm^{-3} deg C^{-1}.

Mechanical analysis of the nest and nearby soil, as well as soil structure studies using soil blocks impregnated with fluorescent wax, are discussed by Ettershank (1968).

RESULTS

A preliminary survey of the range of values to be expected, using mercury-in-glass thermometers, was made in February 1967. (Fig. 1). This indicated that mid-summer temperatures could not be studied with the more accurate electric thermometers. A detailed study was carried out in September 1967, using four temperature probes in the nest and four in the surrounding soil at depths of 2·5, 7·6, 23 and 38 cm and four air temperatures were taken at heights of 5, 10, 20 and 40 cm above ground. Net radiation was recorded, but no flux plates were available for soil heat measurements. Data were collected every half hour for four days, during which time there was virtually no cloud and only gentle breezes. Fig. 2-5 show the nest and soil temperatures for the four days, and Fig. 6-9 the corresponding air temperatures. Fig. 10 and 11 show isotherms for nest and adjoining soil on one day (29.ix.67). Fig. 12 displays the net radiation recorded with average nest and soil temperatures.

Full instrumentation was not available until August 1968, when data on temperature were obtained at two surface stations, 10, 20 and 40 cm depth, both in the nest and in the adjoining soil 1 m from the nest margin. Air temperatures were taken at 10, 20, 40 and 80 cm above ground, and wet bulb temperatures were read at the 10 and 80 cm levels. Net radiation was recorded one metre above the nest, and two flux plates were
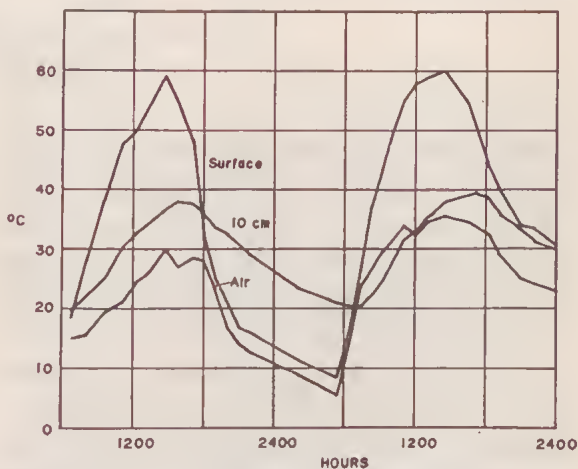

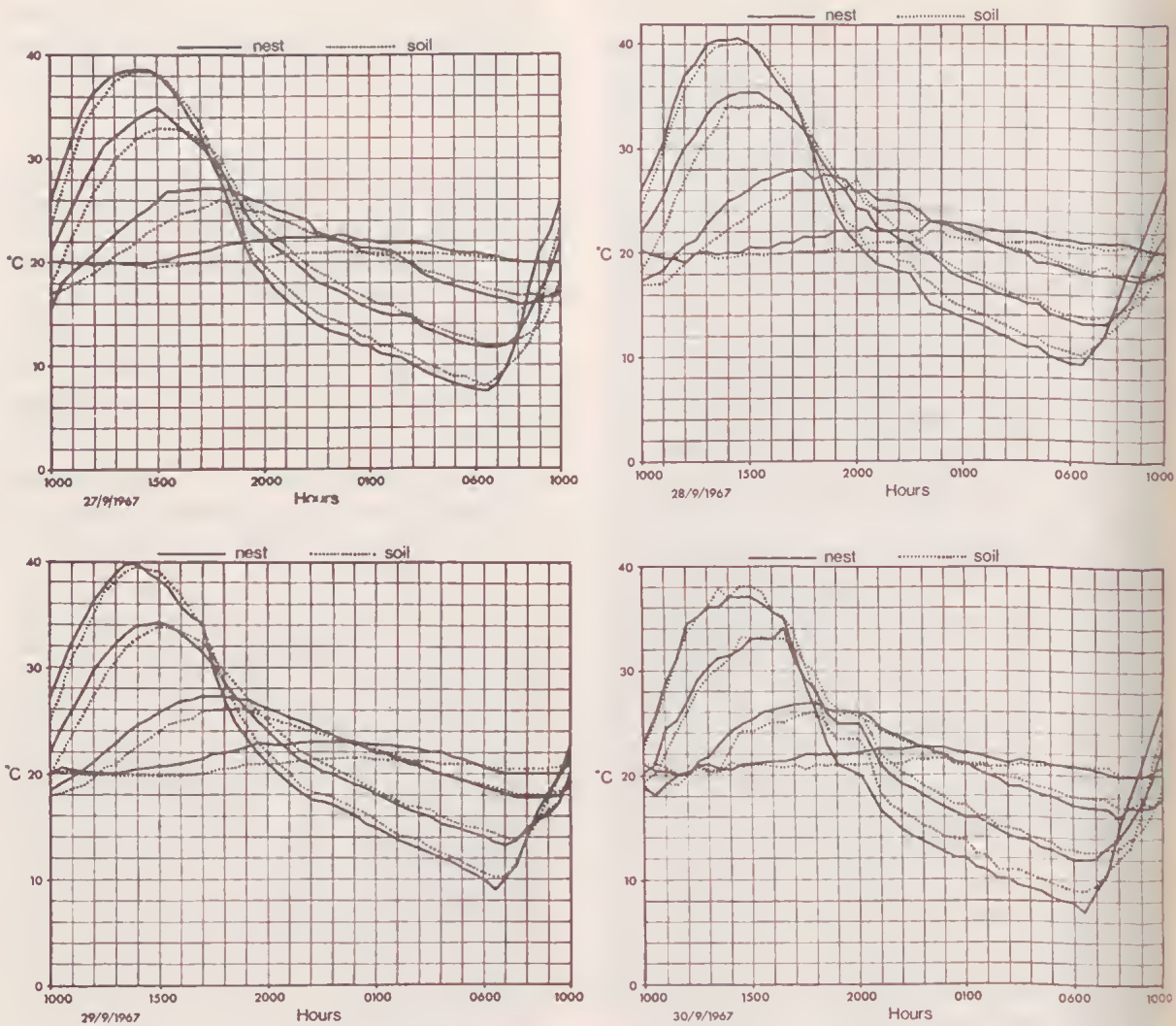Fig. 1—South Ita Sandhills—air, surface and 10 cm temperatures of a meat ant nest in summer (February, 1967).

FIG. 2-5—South Ita Sandhills—2·5, 7·6, 23 and 38 cm temperatures in a meat ant nest and in the adjoining soil: 27-30.ix.67.

installed two days before recording started. Due to weather conditions, only one record exceeding 24 hours was obtained (13-14.viii.68) and these data are presented in full: Fig. 13 shows the nest and soil temperatures, Table 1 selected air, nest and soil temperatures for a particular part of the period (see Discussion) and Fig. 14 the net radiation and soil heat flux.

At the same time, gas and humidity samples were obtained; Fig. 15 presents data for oxygen consumption and carbon dioxide production, calculated on the basis of samples drawn from the respiration hood, and expressed as cubic millimetres of gas per square centimetre per hour, plotted against surface temperature on the nest.

Regression lines of gas volumes on temperature were fitted (Sokal & Rohlf 1969); the slopes of the lines are very highly significant ($p < 0·001$).

Samples of air drawn from the galleries showed the internal state of the nest. The gas composition (stated as mean ± standard error) was oxygen $20·729 \pm 0·0195\%$ and carbon dioxide $0·183 \pm 0·0165\%$. On the other hand, air samples drawn from the respiration hood placed on the ground and from the 'synthetic gallery' were indistinguishable from the normal free air values of oxygen $20·946 \pm 0·002\%$ and carbon dioxide $0·033 \pm 0·001\%$ (*CRC Handbook of Chemistry and Physics*, 48th ed.).

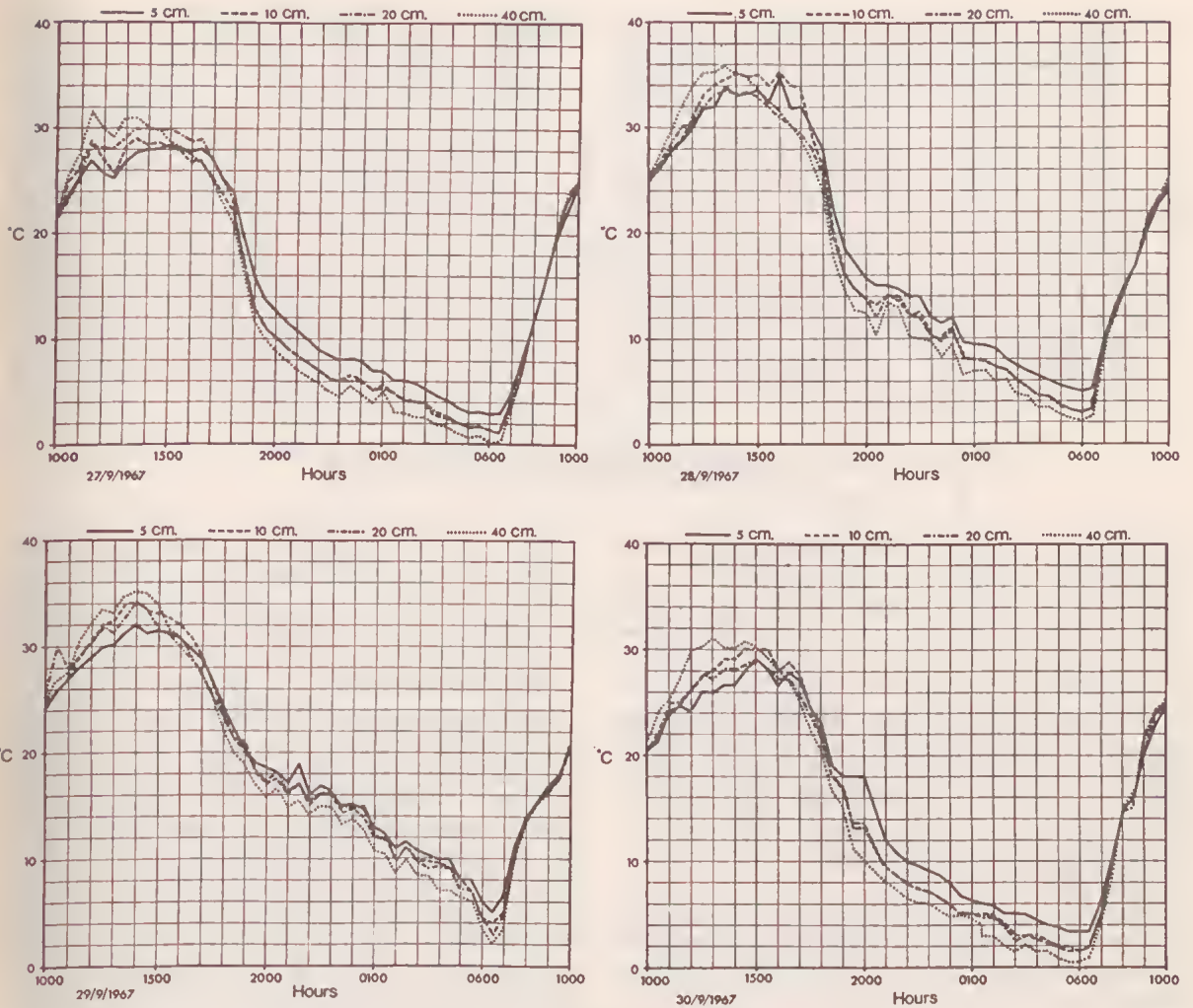Relative humidity in the nest and surrounding

FIG. 6-9—South Ita Sandhills—air temperatures at 5,
10, 20 and 40 cm above ground: 27-30.ix.67.

soil did not seem to be correlated with site, temperature or time of day, and was surprisingly constant (mean ± standard error, $68 \cdot 3 \pm 1 \cdot 63\%$).

Table 2 shows the soil moisture obtained by sampling on 8×8 grids enclosing three nests and part of the soil all around, in the same general vicinity of the nest used for temperature studies. In each case, the samples were classified as nest or soil, and an average moisture calculated for nest and soil samples. These were tested using Student's t, and it will be seen that in each case the nest soil contained more water.

The specific heat of nest soil was $0 \cdot 20$ cal gm^{-1} deg C^{-1}, and the bulk density $1 \cdot 71$ gm cm^{-3}, yielding a thermal capacity of $0 \cdot 34$ cal cm^{-3} deg C^{-1}, while the specific gravity was $2 \cdot 62$; each is the mean of three determinations. The thermal

capacity of the soil two metres from the nest was also $0 \cdot 34$ cal cm^{-3} deg C^{-1}, and the specific gravity $2 \cdot 66$, a trivial difference; these are also based on three determinations from two samples each. Corresponding figures for a nest of the same species from Bacchus Marsh (Victoria), some 800 km south, are: thermal capacity of the nest soil $0 \cdot 34$ cal cm^{-3} deg C^{-1}, but of the gravel covering the nest $0 \cdot 27$; specific heat respectively $0 \cdot 20$ and $0 \cdot 17$ cal gm^{-1} deg C^{-1}; and bulk density, $1 \cdot 72$ and $1 \cdot 57$ gm cm^{-3}.

Table 3 shows the calculated evaporation rates from the nest for the period 8 a.m. on 13.viii.68 to 10 a.m. on 14.viii.68. Rates are given in units of millimetres of water per day: that is the amount of water that would be lost from a freely evaporating water surface receiving the same energy
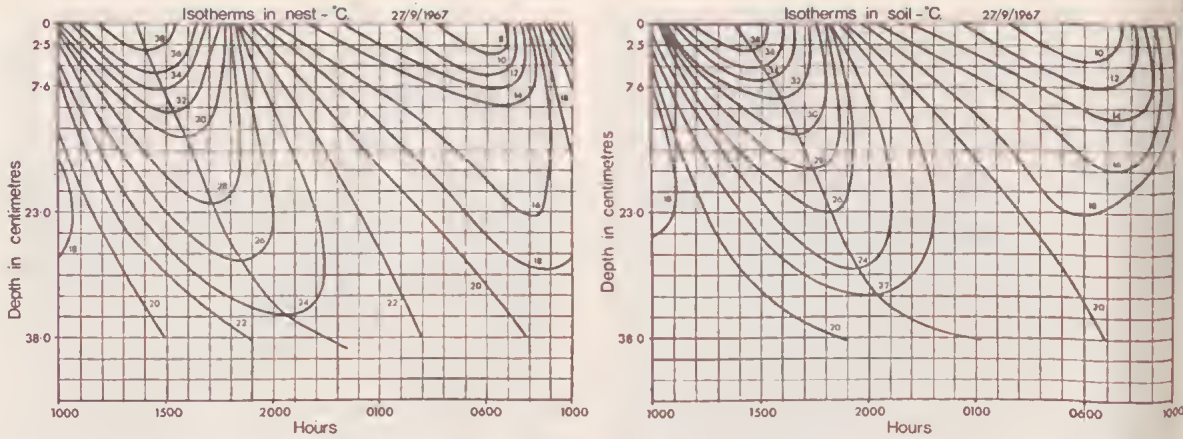
Fig. 10-11—South Ita Sandhills—isotherms in the
nest and adjoining soil for 24 hours: 27.ix.67.

input as calculated from the partitioning of available energy in the soil by the Bowen ratio. In this table, a dash indicates no evaporation; in those entries marked with an asterisk, the gradient of temperatures was not steep enough for reliable computation. The net radiation (R) and heat flux in the ground (G) are also given, in milliwatts per square centimetre, the units used in computation (Slatyer & McIlroy 1961). Moisture content of the nest soil at this time was 2·6%.

DISCUSSION

NEST TEMPERATURE

The close relationship between net radiation and soil temperature is apparent from Figure 12. The net radiation may be seen as the sum of two components:

(i) There is a more or less steady level of outgoing radiation: the Stefan-Boltzman equation (Rose 1966) shows that all bodies emit radiation with a flux density proportional to their absolute temperature, i.e. about 300°C. As the absolute temperature fluctuation of the soil surface is relatively small, either on a daily or yearly basis (and the difference between nest and soil temperature even less), the variation in this component of the radiation equation can be taken as negligible. This may be seen in Figure 12, between 2200 and 0400 hours when there is no incoming radiation. Similarly, Wien's displacement law predicts that the wavelength of maximum emission of this radiation (which is also proportional to the absolute temperature) will be in the long-wave infra-red region of the spectrum, at about 10 microns.
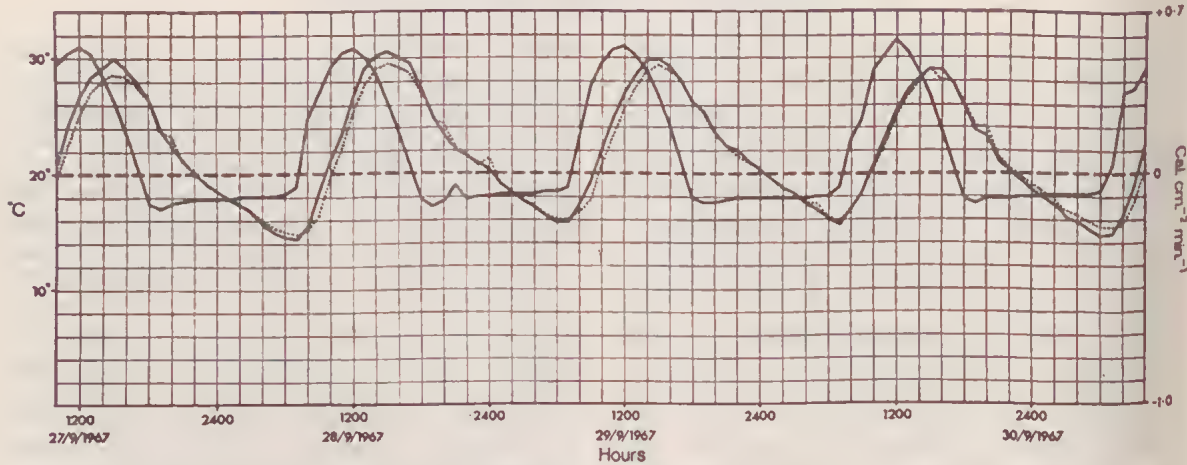

Fig. 12—South Ita Sandhills—net radiation (right ordinate) and average temperature (left ordinate) of nest (solid line) and adjoining soil (broken line): 27-30.ix.67.
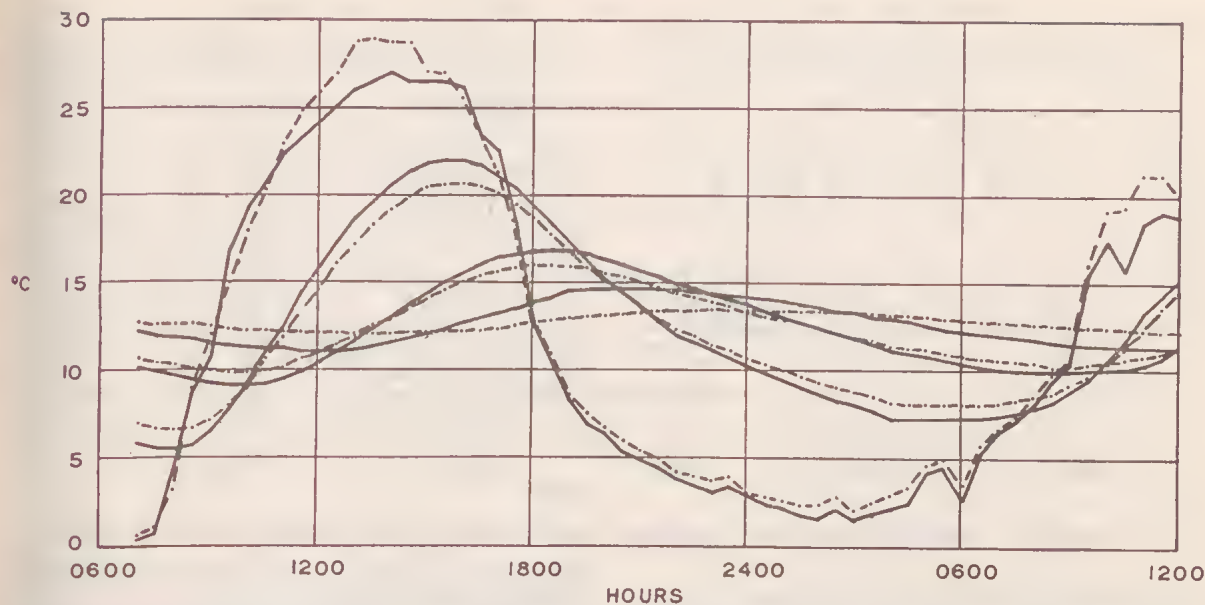
Fig. 13—South Ita Sandhills—surface, 10, 20 and 40 c m temperatures of the nest (solid line) and adjoining soil (broken line): 13-14.viii.68.

(ii) The incoming, short-wave radiation from the sun reaches the surface after attenuation by reflection and scattering in the atmosphere; this component consists of this direct beam of radiation and an indirect quantity known as sky radiation. The radiation impinging on a surface such as the soil is subject to reflection from that surface, and part of the incoming radiation is lost back to the sky—the reflection co-efficient is termed the albedo. Finally, the flux density falling on a horizontal surface is attenuated by a factor equal to the cosine of the angle of elevation of the sun. The resultant flux density measured by a horizontal radiometer is thus a smooth curve, subject to modification by events such as passing clouds or other changes in the optical properties of the atmosphere.

Radiation absorbed by the nest or soil surface causes a rise in temperature. If the soil below is cooler, some of the heat will be conducted downward to successively lower levels in the soil, and the deeper ground temperatures will rise. At the same time, part of this energy is lost from the ground to the atmosphere by sensible and latent fluxes: that is in warming the air above the nest and in evaporating soil water. Thus the temperature attained at any point is the result of the balance struck between heat input, either radiative or conductive, and losses.

Radiative energy input reaches its maximum (on a clear day) when the sun reaches the zenith, at which time the surface temperature is also at or approaching its maximum. After this, the surface temperature begins to drop, but energy is still being transferred down the temperature gradient into the soil; the maximum temperature attained at any depth becomes lower and occurs later as the depth increases (Fig. 2-5). This process is seen most clearly in Figs. 10 & 11; the line cutting across the isotherms, joining their deepest points, is a measure of the speed of transmission of heat through the soil: it is curved, rather than the straight line expected, because the soil is not homogeneous in its heat transmission characteristics.

When the surface becomes cooler than the deeper levels at night, the direction of heat flow is reversed. This is apparent from Fig. 14, which shows the net radiation of the nest (the greater amplitude curve) and the soil heat flux. Heat flowed into the nest from 0845 in the morning until 1730 in the afternoon, after which stored energy started to pass back to the surface. Two additional points of interest arise from this figure. Between 0300 and 0400 in the morning, the radiation loss quite suddenly decreased. This coincided with the arrival of a metereological frontal system; observations recorded at the time show no cloud until 0300, when 1/8 cloud cover was recorded in the southwest, 4/8 at 0330 and 7/8 at 0430, which continued, with a short break at 1600, for the remainder of the period. The clear sky is an acceptor of long wave radiation, whereas cloud reflects back a considerable part.
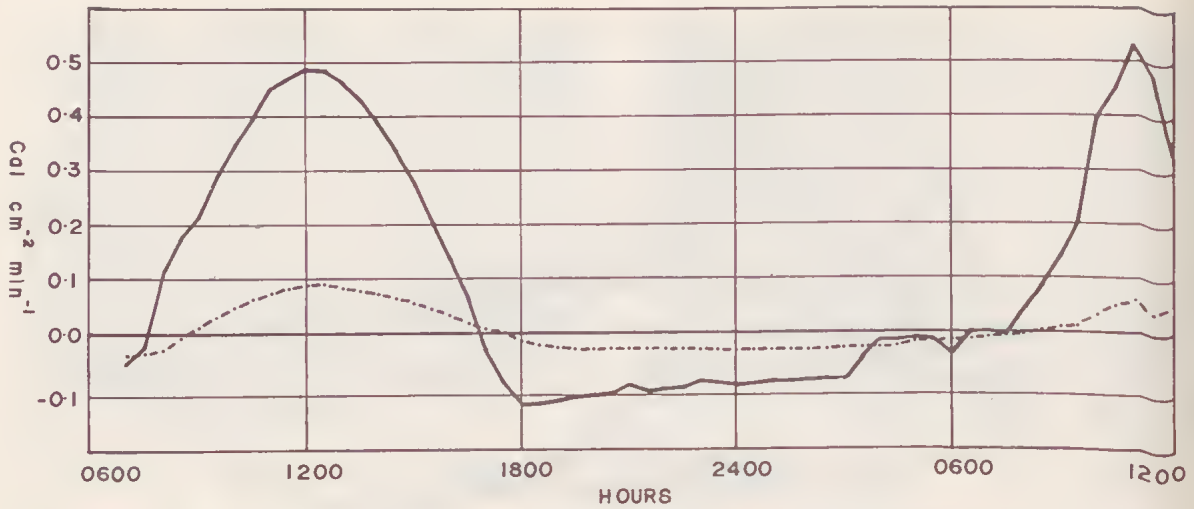
FIG. 14—South Ita Sandhills—net radiation (solid line) and soil heat flux over 30-hour period: 13-14.viii.68.

Integration of the soil heat flux curve (Fig. 14) shows that in this period, 27·73 cal cm^{-2} passed down through the flux plates, but only 22·56 cal cm^{-2} passed up. The difference, 5·17 calories, means that the temperature at this level, 5 cm below the surface, should be 3·04°C higher on 14.viii.68 than on the previous day (calculated from the experimentally obtained thermal capacity). Interpolating from the temperatures at the surface and 10 cm (Fig. 13) the observed temperature difference is 3·03°C.

It will be seen that the ants have, at most times, levels in the nest at which the temperature should be satisfactory for their various functions: higher temperatures for incubating brood near the surface in the day, and a warm zone lower in the nest at night. Most of the galleries are clustered in the upper 25 cm of the nest, so it would appear that this region is satisfactory for their activities. Below 25 cm, the nest consists of a relatively few deep shafts with occasional side galleries, in which most of the population is to be found during cold winter conditions (Ettershank 1968). This author also estimated that the galleries occupy 8-10% of the volume of the upper part of the nest; as the heat input to the nest and to the surrounding soil is the same, it would be expected that the temperature rise in the nest would be about 10% more, and this can be seen in Fig. 2-5, & Fig. 13. Note also that the deep temperature in the nest is above that in the soil, a positive benefit for the occupants. The expected, more rapid rate of heating in the nest can also be observed. However, the nest surface is cooler during the day (Fig. 13); this is discussed below in reference to the nest surface and decoration.

SOIL MOISTURE

The three large sampling trials conducted showed higher soil-water levels in the nest than in the surrounding soil (Table 2).

Rates of water loss, calculated from the energy data and the Bowen ratio, apply to large areas, not local patches (Slatyer & McIlroy 1961). Water loss from a surface depends on there being a source of heat to supply the latent heat of vaporization (590 cal gm^{-1}); on the vapour pressure of the overlying air being maintained at less than that of the evaporating surface (that is, water vapour, like heat, must pass down a gradient, since evaporation is a net transfer of water molecules); and finally, there must be a continuing supply of water available for evaporation, and so drier soils impose a limiting factor (Rose, 1966). Generally, evaporation can be expected to continue while energy is available, i.e. when $R - G$ (Table 3) is positive. Evaporation did take place over much of the day, but not in the middle of the day, presumably because all the available water had been removed and a recovery period was necessary. This effect was observed on on the five other days for which partial records were collected. $R - G$ may be positive at night, but then no vapour gradient may be present. It should be noted that the accuracy of these energy balance computations are dependent on a reasonable vertical gradient between the measuring sites. Slatyer & McIlroy (1961) suggested as a rule of thumb that the gradient should be twenty times the accuracy of the measuring instrument, which in this case would thus be 1°C. Also, the model was developed initially for free water surfaces,

TABLE 1

SOUTH ITA SANDHILLS—selected Air and Surface Temperatures 14/viii/68 (*see text*)

Time	10 cm Air Temperatures (°C)		Surface Tmperatures (°C)	
	Dry bulb	Wet bulb	Nest	Soil
0030	0·70	0·52	2·30	2·70
0100	0·90	0·55	2·22	2·66
0200	0·10	0·10	1·55	2·30
0300	0·10	0·10	1·31	1·97
0330	0·25	0·25	1·78	2·25
0400	1·01	1·01	2·04	2·69
0430	1·64	1·62	2·52	3·20
0500	3·27	2·95	4·14	4·53

TABLE 2

SOUTH ITA SANDHILLS—mean percentage water content of nest and soil samples at three sites (64 samples from each site); number of samples from nest and soil at each site is shown in brackets.

Site	Nest	Soil	Significance
1	2·1% (20)	1·9% (44)	*
2	1·3% (14)	1·1% (50)	*
3	3·4% (23)	3·1% (41)	*
Overall Averages	2·3%	2·0%	

TABLE 3

SOUTH ITA SANDHILLS—radiant and soil heat fluxes, and calculated evaporation rate.

Date	Time	R mW cm^{-2}	G mW cm^{-2}	E mm H$_2$O day^{-1}
13.viii.68	0800	7·99	—4·10	—
	0900	14·74	1·61	8·1
	1000	24·25	6·41	30·7
	1100	31·41	9·16	4·2
	1200	33·97	12·22	—
	1300	32·26	11·26	—
	1400	27·24	10·24	0·4
	1500	19·34	7·28	0·8
	1600	9·42	4·54	1·1
	1700	—2·23	0·52	—
	1800	—9·51	—2·28	— *
	1900	—8·82	—3·93	— *
	2400	—6·57	—4·76	— *
14.viii.68	0400	—2·22	—3·82	— *
	0500	—1·55	—2·61	— *
	0600	—3·74	—3·05	— *
	0700	0·00	—1·11	— *
	0800	2·95	—0·32	2·2
	0900	4·80	0·92	4·6
	1000	27·46	4·86	—

and only later applied to agricultural problems. In consequence, investigations of the model, in which the calculated losses were checked against a lysimeter, have been restricted to soils with a higher water status, and its application to drier soils, though satisfactory in theory, has not been rigorously tested.

Air movements parallel to the ground surface in such sparsely vegetated areas ensure that conditions over any area are fairly uniform, that is that there will not be small pockets with abnormally high or low temperatures or humidities. The figures quoted in Table 3 should be an unbiased estimate of conditions over much of the surrounding countryside. At ground level, however, it can be seen from Figure 13 that the nest surface temperatures are below those of the surrounding soil. A sample of these data, for 13.viii.68, is shown in Table 1. From these, it will be seen that for three hours in the early morning the air at 10 cm is at dew point; this is a regular feature of desert environments. Dew tends to impinge on the coolest objects in an area and on slightly elevated objects (Slatyer & McIlroy, 1961), and the surface of the nest fulfils both these qualifi-

cations. If, as is likely, the air flow at the surface is at the same temperature as the general soil surface and the air is saturated (Geiger, 1965), then the surface of the nest will be below dewpoint and dew will immediately form on it. The nest soil would rapidly absorb it, reducing the chance of re-evaporation.

Now, most of the water 'falling' as dew does not come from any height in the atmosphere, but instead from distillation from the ground, and thus generally speaking there is little or no overall gain from dewfall over any large area (Geiger, loc. cit.). In this case, however, it is proposed that the nest is gaining dew at the expense of the surrounding area. Slatyer & McIlroy show on theoretical grounds that the maximum possible rate of condensation would be 0·07 to 0·15 mm hr^{-1}, and state that the maximum reliably recorded rate of dewfall for one night was 0·5 mm, although the conditions were not given. If the nest does act as a focus of condensation, input locally could be higher. The gradient of soil moisture in the nest was not studied, but it can readily be calculated that to maintain the higher water status observed in a 25 cm column of nest material

would require an input differential to the nest of 0·75 mm of dew per cm² per night. Some form of lysimeter would be needed to demonstrate this model, and this would hardly be practical in an ant nest.

Diem (1937) has shown experimentally that sandy soils 'breathe' a volume of air each day equivalent to a column 22 m high; Geiger (1965) points out the importance of the water in this transpired air. Moist atmospheric air will give up moisture to the soil if this is colder, and he terms this 'internal dew'. For the nest to gain the 0·3% differential observed, it would also have to absorb the latent heat of vaporization of the water, amounting in this case to 44 calories cm^{-2}, which would give a 5°C rise in the 25 cm column of soil if it were all released at once. Over a period of some hours, of course, the effect would hardly be visible in the overall heat economy of the nest.

Chaptal (1932), in a little-noticed paper, showed that viticultural soils in the south of France gained 2000 m³ of water per hectare more than could be accounted for by rainfall or movement of soil water, and showed that this was probably acquired by adsorption of water molecules to the soil in a similar process of soil transpiration. He was able to show, furthermore, that much of this fixation of water by the soil occurred between 2 p.m. and 6 a.m. when the subsurface soil was warmer than the air, so this was not simple condensation of dew. It is interesting that the surface of the meat ant nest is perforated with entrance holes, the content of coarse sand is increased compared with the surrounding soil (Ettershank, 1968) and the bulk density may be slightly lower (possibly due to working by the ants), all of which should increase ventilation and fixation of water.

On a much larger scale, Chaptal discussed the report of a group of engineers who found that certain natural springs result from condensation inside severely fissured geological formations overlying an impervious bedrock. He quotes a communication to the French Agricultural Academy from a H. Hitier on the investigation of the 13 'aerial wells' of the ancient Greek settlement of Theodosia, in the Crimea, which consisted of pyramids of calcareous stones measuring 30 × 25 × 10 metres. Conduits from these to the town are claimed to have supplied 720 m³ of potable water per day. Chaptel describes a model of these that he built, which delivered a maximum of 2·528 litres per day.

Winterkorn (1955) found that a similar phenomen was responsible for swelling and buckling of some road foundations.

SOIL HUMIDITY

Air in the galleries is presumably in equilibrium with the soil, and shows a fairly constant value around 68% (confirmed for a nearby locality by D. Shorthouse, pers. comm.).

NEST METABOLISM

Gas analysis of air aspirated from the nest shows that the ants breathe air somewhat depleted of oxygen (−0·217%) and enriched with carbon dioxide (+0·15% or 4·5 times the level in free air) as shown above. No work has been done on the physiological response of ants to high levels of carbon dioxide; the usual response in insects is to open the spiracles through relaxation of the spiracular closing muscles, an endogenous property of this muscle in the presence of high levels of dissolved carbon dioxide (Wigglesworth, 1965). This would seem inappropriate in an animal that normally lives under such conditions, particularly as the relative humidity in the nest is only 68%, but the action of the spiracular occluder cannot be seen from the outside on an intact ant, so this is not easily studied.

Two methods were used to check the fidelity of the respirometer hood method. Firstly, oxygen absorbent was injected into the soil under a hood on the ground to a depth of 10 cm; at the same time an equal volume of absorbent was injected into a 250 ml flask fitted with a horizontal burette partly filled with an indicator fluid. In two trials 8·25 ml of oxygen was absorbed in the flask when 8·64 was accounted for in the air sample drawn from the hood during 25 minutes; for the second trial, the corresponding figures are 6·60 and 6·51. Secondly, carbon dioxide levels under the hood could be checked against the observed, laboratory determined respiratory quotient of 0·78 (Cutress and Ettershank, unpublished data). At 20°C, the oxygen consumption calculated from the regression line is 21·23 mm³ cm^{-2}, for which the predicted carbon dioxide production is 16·30 mm³ and from the RQ is 16·56 mm³. The correspondence is not as good at lower temperatures, possibly due to slower diffusion of the carbon dioxide.

Whether the nest can be used as a natural calorimeter (Englemann, 1966) can be answered from the respirometry data. At the respiratory quotient of 0·78, one cubic centimetre of oxygen consumed in metabolism releases 4·73 calories of heat (Southwood, 1966), so 18 mm³ cm^{-2} hr^{-1} represents 0·086 cal cm^{-2} hr^{-1}. (Note that Southwood (1966) drew the data for this table from the classical book by Brody (1945), as have many authors since. Now Brody adopted a convention: 'calories' meant the normal CGS unit, but 'Calories' meant kilocalories. Southwood ap-
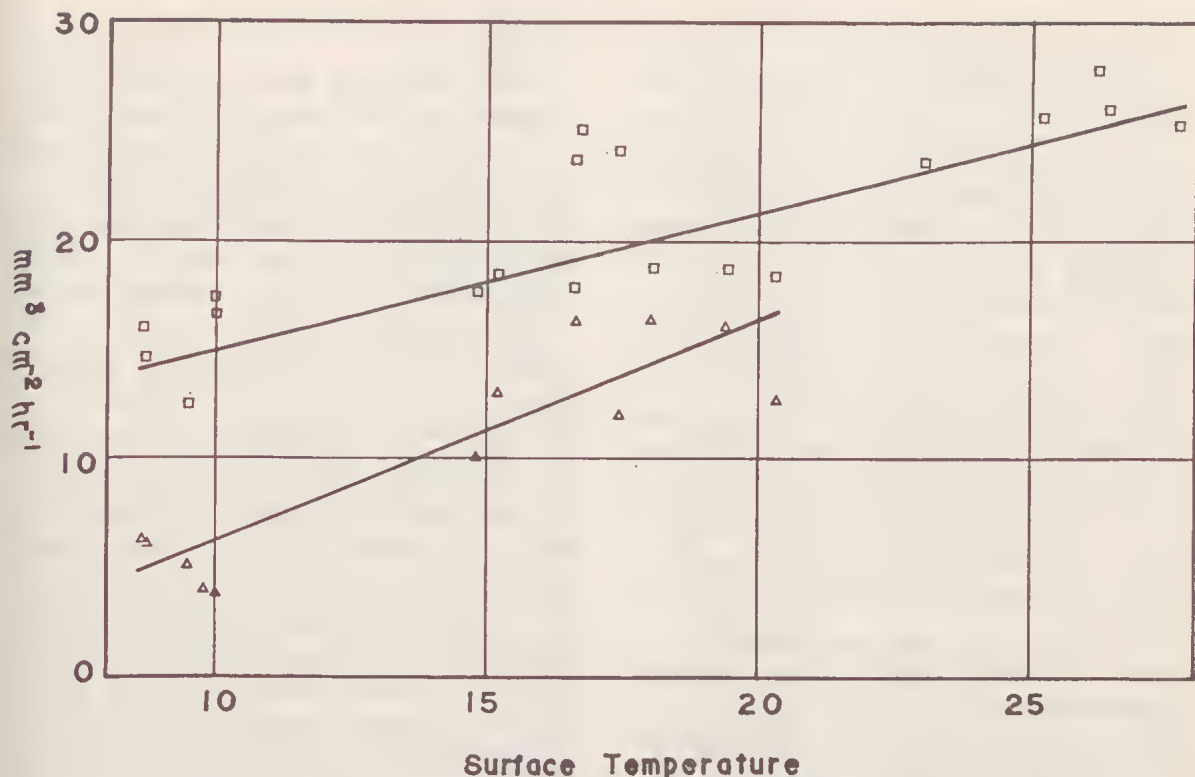
Surface Temperature

Fig. 15—South Ita Sandhills—oxygen consumption (squares) and carbon dioxide production (triangles) of a meat ant nest, against temperature. Equations to the lines are $Y_{O_2} = 8.60 + 0.63X$ and $Y_{CO_2} = -3.77 + 1.00X$, where X = temperature in $°C$.

parently missed this, so that his figures are wrong by a faetor of 1000.) With a thermal eapaeity of 0.34 eal em^{-3} deg C^{-1}, this would raise the temperature of one eubic eentimetre of soil by $0.25°C$ per hour. With the present probe spaeing, this would not be deteeted, and in any event, ehanges of this magnitude could easily be swamped out by the perturbation of a passing eloud. Thus this approach is eonsidered to hold little promise.

Using the respiromctry data, an estimate of the overall metabolie activity of the nest may be obtained. The surface area of the nest is 4.93 m^2, so the overall oxygen eonsumption at $20°C$ is 1.047 1 hr^{-1}. This is equivalent (Southwood, 1966) to the produetion of 5 kiloealories per hour; to aehieve this, the oeeupants of the nest would need to metabolize 1.35 grams of glueose, 0.87 g of erude protein or 0.53 g of fat. At $10°C$, the oxygen eonsumption would be 0.701, produeing 3.3 Keal per hour, for which the respee-tive substrate equivalents are 0.90 g, 0.58 g and 0.35 g.

Ettershank (in press) found that this ant eon-sumed 1.66 ml O_2 per 100 mg dry weight per day at $21°C$. Thus the above data would indieate 1.5

of dry weight of ants in the nest or 4.5 kg wet weight, or about 300,000 individual ants. This is of the same order of magnitude of an estimate based on data by Greaves (pers. eomm.) from exeavation and eounting of nests in the Can-berra area, allowing for the larger size of the ants at South Ita.

Ettershank (in press) also found, using a minia-ture bomb ealorimeter, that the meat ant was equivalent to some 5.5 Keal gm^{-1} dry weight; thus the standing erop of meat ants in the nest is exeavation and eounting of nests in the Can-estimated at 8250 Keal.

NEST SURFACE

The most striking feature of meat ant nests is the 'deeoration' of the surfaee, noted by every author who writes about this speeies. Small peb-bles, and particularly ironstone soil nodules, mea-suring 2 to 4 mm seem to be the preferred ma-terial for eovering the nest, partieularly around the eoast and in the mountains; on the inland slopes leading baek from the Great Dividing Range, pebble deeoration slowly gives way to use of plant parts together with a greater or lesser amount of pebble: small twigs, leaf petioles,

gumnuts and chopped-up grass stems are all used (Ettershank, 1968).

On one nest observed by the present author at Nyngan, N.S.W., on an extensive silt plain where no pebbles could be found, and plant fragments seemed sparse also, the ants had acquired the broken-up crust formed by the action of rain on the surface of the soil, and arranged these pieces over the surface of the nest. At all times when the workers are active, some may be found re-arranging the decoration on the nest, moving pieces so that the distribution appears to the human eye to be very regular. Many returning workers carry pebbles or plant parts.

The decoration would appear to fulfil a number of functions, which are listed below. Whether any particular one was the object of intense selection during the evolution of this nest form (seen also in desert species in North America) can only be speculation; of the four, however, mechanical protection would seem the most basic. The suggested functions are:

(i) The decorated area differentiates a behavioural boundary: large vertebrate intruders onto the nest area are pursued and attacked vigorously by the workers, but outside the decorated area, the intensity of pursuit diminishes sharply, and few workers will persist in following the intruder a metre from the nest area. Attackers attached to the intruder continue to bite, however, until mechanically removed. The ground-level attack, incidentally, is visually oriented, for the attacking phalanx of workers will follow any large object after being provoked.

(ii) The decoration protects the surface from rain erosion. The ants build up collars around the entrance holes *before* storms, and narrow the entrances down until only a single ant can pass through at a time; decoration material is often moved onto these collars. As soon as the sun starts to shine after a heavy downpour, the collars are removed and the entrance holes are opened up to 1·5 to 2 cm. If gravel is removed from a nest during a severe rain-storm, rain erosion may be seen and occasionally gallery roofs are broached.

(iii) By presenting an aerodynamically 'rough' surface, the decoration causes turbulence and prevents laminar air flow over the nest surface, which would reduce the rate of heat transfer by several orders of magnitude (Rose, 1966; Slatyer & Me-Ilroy, 1961). In Fig. 13, it is apparent that the immediate surface layer of the nest is cooler than that of the adjoining soil, although at all levels below ground the nest is warmer; this must be attributed to turbulent cooling at the surface. It is notable that at night the nest surface temperaure parallels the soil surface temperature, but is 0·5 to 1·0°C cooler.

On the other hand, a heavy gravel covering is found in areas with lower daytime temperatures. The gravel, having a lower thermal capacity, heats more rapidly than would an exposed soil thereby creating a sharper gradient into the soil; the upper temperature reached is still about the same, but the heating curve is steeper, giving the colony a longer period each day on a more favourable temperature regime.

(iv) The decorative fragments would present a greater area for dew deposition, as discussed above.

Finally, there is a seeming paradox in a desert ant constructing a mound nest, which will receive greater insolation (Steiner, 1929) and increase the heat burden of the colony in summer. It is distinctly advantageous in cold areas, and higher mounds are seen in mountain areas (Greaves, 1939). For the desert ant, it may be advantageous in winter, when the heating curve, at least of the eastern side of the nest, will be steeper allowing activity and foraging to start a little earlier, but ants deeper in the nest would already be at 'working temperature', and any advantage would be lost as soon as the ant leaves the surface of the nest. Other ant species excavate quite large nests and dispose of the spoil—the meat ant actually brings in extra material and incorporates it into the nest. This paradox is elucidated if the functions of the mound discussed above are accorded to it: that it acts as a focus for dew deposition and as a surface for heat dissipation through turbulent cooling. Paradoxes in biology are usually in the mind of the observer: evolution does not lead to insoluble enigmas.

CONCLUSIONS

1. The use of a net radiometer, soil heat flux plates and thermistor thermometer probes enables a close study of the temperature regime in an ant nest; the fate of incident solar heat can be followed and quantitatively accounted for when other soil parameters (such as thermal capacity) have been obtained. Partition of the heat budget allows estimates of the rate of water loss from the soil.

2. The nest passes through a cycle of heating and cooling each day; temperature excursions are greatest at the surface, decreasing with depth. This cycle is modified by the nest structure compared with the soil nearby, and all levels show slightly greater excursions, except the surface which benefits from turbulent cooling.

3. Soil moisture is slightly higher in the nest, and it is suggested that this is maintained through

differential capture of dew, at the expense of the surrounding soil.

4. The relative humidity of the air in the nest is similar to that in the surrounding soil—despite the higher nest temperature—at around 68%.

5. Ants in the nest live in an atmosphere enriched some 4·5 times with carbon dioxide and slightly depleted of oxygen.

6. Collection of gases in a hood over the nest gave a measure of the overall respiration. From this data, it is concluded that temperature measurements of the nest, treating it as a natural calorimeter, could not be used to estimate respiration. Energy consumed in respiration was found from gas analysis to be 5 Kcal hr^{-1} for a 4·9 m^2 nest at 20°C and 3·3 Kcal hr^{-1} at 10°C.

7. As the respiration rate per ant was known, the population was estimated to be 1·5 kg dry weight, or about 300,000 individual ants, equivalent to 8250 Kcal standing crop in the nest.

8. The 'decoration' on the nest was found or presumed to subserve several functions: a behavioural boundary, a mechanical protection, a modifier of surface temperature and a dew trap.

9. The logical dilemma of reconciling a heat-gathering mound nest with a desert environment is solved by examining the advantages accruing from this type of construction.

ACKNOWLEDGMENTS

REFERENCES

ANONYMOUS, 1956. Control of two ant pests. *Rural Res. C.S.I.R.O.* 16: 14-20.

BRODY, S., 1945. *Bioenergetics and Growth*. Reinhold, N.Y.

CHAPTAL, L., 1932. La lutte contre la sécheresse: la captation de la vapeur d'eau atmosphérique. *Nature, Paris* 2892: 448-54.

COLE, A. C., 1932. Observations on semi-desert ants. *Ohio J. Sci.* 32: 533-38.

DENNIS, C. A., 1938. The distribution of ant species in Tennessee with reference to ecological factors. *Ann. ent. Soc. Amer.* 31: 267-308.

DIEM, M., 1937. Bodenatmung. *Beitr. Geophys.* 51: 146-66.

DUNCAN-WEATHERLEY, A. H., 1953. Some aspects of the biology of the mound ant. *Iridomyrmex detectus* Sm: *Aust. J. Zool.* 1: 178-92.

ELLIS, R., 1966. The Koept field respirometer. In *Conference on Instrumentation for Plant Environ-*

ment Measurements, ed. D. E. Angus. Society of Instrument Technology, Melbourne.

ENGLEMANN, M. D., 1966. Energetics, terrestrial field studies, and animal productivity. In *Advances in Ecological Research*, Vol. 3, ed. J. B. Cragg. Academic Press, London and N.Y.

ETTERSHANK, G., 1968. The three-dimensional gallery structure of the nest of the meat ant, *Iridomyrmex purpureus* (Sm.). *Aust J. Zool.* 16: 715-23.

GEIGER, R., 1965. *The Climate Near The Ground*. Harvard University Press, Harvard, Mass.

GOLLY, F. B. & GENTRY, J. B., 1964. Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. *Ecology* 45: 217-25.

GREAVES, T., 1939. The control of meat ants (*Iridomyrmex detectus* Sm.). *J. Conn. scient. ind. Res. Aust.* 12: 109-14.

KOEPT, H. von., 1952. Laufende Messung der Bodenatmung im Freiland. *Landtech. Forsch.* 4: 186-95.

NEL, J. J. C., 1965. Influence of temperature and relative humidity on water loss in the workers of the meat ant, *Iridomyrmex detectus* (Sm.). *Aust. J. Zool.* 13: 301-15.

PHILIP, J. R., 1961. The theory of heat flux meters. *J. Geophys. Res.* 66: 571-9.

PLATT, R. B. & GRIFFITHS, J. F., 1964. *Environmental Measurement and Interpretation*. Reinhold Publishing Corp., New York.

ROSE, C. W., 1966. *Agricultural Physics*. Pergamon Press, London.

SAUNDERS, G. W., 1967. Funnel ants (*Alphaenogaster* spp., Formicidae) as pasture pests in North Queensland. I. Ecological background, status and distribution. *Bull. ent. Res.* 57: 419-32.

———, 1969. II. Control. *Ibid.* 59: 281-90.

SCHOLANDER, P. F., 1947. Analyser for accurate estimation of respiratory gases in one-half cubic centimeter samples. *J. biol. Chem.* 167: 235-50.

SLATYER, R. O. & McILROY, I. C., 1961. *Practical Microclimatology*. UNESCO. Paris

SOKAL, R. R. & ROHLF, F. J., 1969. *Biometry*. W. H. Freeman & Co., San Francisco.

SOLOMON, M. E., 1957. Estimation of humidity with cobalt thiocyanate papers and permanent colour standards. *Bull. ent. Res.* 48: 489-506.

SOUTHWOOD, T. R. E., 1966. *Ecological Methods*. Methuen, London.

STAHEL, G. & GLIJSKES, D. C., 1941. Weitere Untersuchungen über Nestbau und Gartenpilz von *Atta cephalotes* L. und *Atta sexdens* L. *Revista Ent.*, Rio de J. 12: 243-68, 766-75.

STANDARDS ASSOCIATION OF AUSTRALIA, 1966. *Testing Soils for Engineering Purposes—Australian Standard A89-1966*, Sydney, N.S.W.

STEINER, A., 1929. Temperaturuntersuchungen in Ameisennestern mit Erdkuppeln, im Nest von *Formica exsecta* Nyl. und in Nestern unter Steinen. *Z. vergl. Physiol.* 9: 1-66.

SUDD, J. H., 1967. *An Introduction to the Behavior of Ants*. Edward Arnold, London.

WIGGLESWORTH, V. B., 1965. *The Principles of Insect Physiology*. Methuen, London.

WILLIAMS, C. B., 1954. Some bioclimatic observations in the Egyptian desert. In *Biology of Deserts*, ed. J. L. Cloudsley-Thompson. Institute of Biology, London.

WINTERKORN, H. F., 1955. A research program on the aerial well. *Engrs' Bull. Colo. Soc. Engrs* 39: 10-11, 23.